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SHORTER ARTICLES AND DISCUSSION

THE DUALITY OF EGG-SECRETION

There are two properties of egg-secretion which have attracted particular attention. One of these is the power of agglutinating spermatozoa (Lillie[1]); the other is the power of activating the egg (auto-parthenogenesis, Glaser[2]). These effects have been studied separately, but under normal conditions both must bear, in close affiliation, upon the events of fertilization.

I

We are still in the stage of hypothesis. We know that without exudates fertilization does not take place. This was first demonstrated by F. R. Lillie (*loc. cit.*), who removed the exudates. These, as I found later, can be rendered ineffective without removal, by the presence of charcoal.[3] In neither case is fertilization possible. We also know, from the investigations of Lillie, that the agglutinating agent can be neutralized in two ways: either by spermatozoa, or, by some derivative from the egg itself. Inasmuch as fertilization is prevented by this derivative, Lillie has called it "anti-fertilizin."

Lillie also discovered that the blood of the sea-urchin (*Arbacia*) has preventative effects, but these are different from those of "anti-fertilizin." There is in this case no interference with the agglutination reaction; yet the egg remains unactivated.

Miss Woodward[4] and I (*loc. cit.*) have extended the list of inhibitors to include such diverse things as the pigmented substances derived from testicular tissues; fatty and aqueous extracts of the eggs; and now, oleic acid and olive oil. However I shall consider further only the inhibitors discovered by Lillie.

II

These, together with the fact that the exudates are necessary in normal fertilization, are the foundations of the fertilizin hypothesis. According to this view, egg-secretion contains a body with two bonds; one normally unites with a sperm-borne valence; the other, with a valence borne by the egg. Agglutination is a symptom of the first union; activation of the egg, a symptom of the second. ''Anti-fertilizin'' occupies the agglutinating valence and hence the normal union of sperm and fertilizin is rendered impossible. The inhibitor in the blood, on the other hand, is effective because it binds the second valence of the fertilizin which in consequence cannot unite with its normal receptor in the egg. In the language of Ehrlich, fertilizin is an amboceptor with ovophile and spermophile side-chains; and, normal fertilization involves the formation of a chemical compound which, written in linear fashion, can be thought of as sperm-receptor—spermophile side-chain-ovophile side-chain—egg-receptor.

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[1] *Science,* Vol. 38, pp. 524–528.

[2] *Biological Bulletin,* Vol. 26, pp. 387–409.

[3] The use of charcoal was suggested to me by Dr. G. H. A. Clowes.

[4] *Journal of Experimental Zoology,* Vol. 26, pp. 459–501.

The keystone of the hypothesis is the amboceptor. It symbolyzes the effects of the secretion on spermatozoa and the effects on eggs; it symbolizes also the information gotten from the two inhibitors—the one that prevents agglutination and fertilization and the other which prevents merely fertilization. The amboceptor stands vaguely for the recognized duality of the secretion. The question is, can we precipitate the amboceptor from the realm of the symbolic and bring it within the sphere of the commoner conceptions of physics and chemistry?

III

First of all, are we compelled to think in terms of the amboceptor? The alternative, of course, is a two-body view. Lillie's book,[5] (p. 231) decides against this because there is ''a parallel between absence or loss of agglutinating substance and the capacity of the egg for being activated. The same results would be attained if there were two substances concerned . . . but since the two effects . . . appear and disappear together . . . the writer assumed that they may be regarded as due to a single complex substance.'' Again (p. 232), in discussing the effects of the inhibitors, Lillie writes:

> This still does not prove that sperm agglutination and egg activation are due to the action of a single substance, but it shows again by a different method that the capacity for producing both effects is present

[5] ''Problems of Fertilization,'' University of Chicago Press, 1919.

simultaneously in the egg secretion and the assumption of a single substance is the simplest hypothesis.

A much stronger argument for the one-body view can be advanced. "Anti-fertilizin," by hypothesis, prevents normal fertilization by occupying the spermophile side-chain; yet, "anti-fertilizin" also prevents auto-parthenogenesis (Woodward). This, we might suppose, would indicate a relationship between the two side-chains, such that removal from the reaction system of the one also results in the removal of the other. This state of affairs is actually realized under certain conditions. For example, I have been able to isolate from charcoal materials with agglutinating and activating properties. However, if we infer from these observations, a single body, the reaction of "anti-fertilizin" with fertilizin can hardly serve as evidence that the latter has two side-chains.

IV

In 1918, Miss Woodward[4] reported experiments that bear intimately on the problem. By saturating *Arbacia* secretion with $(NH_4)_2SO_4$ she secured a white flocculent precipitate which after purification by dialysis proved to have very intense agglutinative powers but no capacity for initiating the development of the egg. She called this precipitate, agglutinin.

An initiatory agent, also, was precipitated. $BaCl_2$ was added to the secretion and after removal of the sea-salts, the primary deposit was treated with $N/10$ HCl. As soon as the acid had been freed from $BaCl_2$, acetone was used in excess to bring down a second precipitate, heavy and flocculent. This, after purification with absolute alcohol and ether, dried as a white powder, soluble in both sea-water and distilled.

This second precipitate had marked parthenogenetic effects, but no power to agglutinate sperm. Miss Woodward called the substance, lipolysin, a name which, as I shall show elsewhere, is justified since the material accelerates the hydrolysis of fats.

V

What bearing have these precipitations on the issue? According to Lillie's book, p. 240, "separation under the conditions of chemical analysis may possibly denote a splitting of a single substance of the normal egg."

A. THE AMMONIUM-BARIUM PRECIPITATIONS

1. The agglutinin can be salted out with $(NH_4)_2SO_4$; the lipolysin can be brought down with $BaCl_2$. If we divide a given exudate into two portions, we can precipitate in one, first the agglutinin and later the lipolysin, whereas with the other fraction we can proceed in a manner exactly the reverse.

2. Precipitation in the two cases differs inasmuch as the effective concentration of the $BaCl_2$ is $N/7.5$; that of the $(NH_4)_2SO_4$ in the neighborhood of $5N$.

If precipitation in the two instances is uncomplicated by chemical unions between precipitate and the reagents used to produce them, the case is decisive for the two-body view since it is unlikely that a molecule can be split chemically, merely because one part has solubilities different from those of another part. However, the case is probably not so simple. Very possibly we are dealing with ammonium agglutinate and barium lipolysinate. If this is true, then all we can say is that the amboceptor, present by hypothesis at the outset, breaks down between the agglutinating and the activating valence no matter which of the two groups is bound first.

B. THE CHARCOAL METHOD

Charcoal removes practically the entire organic reaction system. This can be recovered in its essential parts, by subsequently treating the charcoal with $N/10$ HCl. From the clear solution so gotten acetone throws down a voluminous precipitate in two well-marked stages: the first fraction, without agglutinating powers, is lipolytic; the second strongly agglutinates the sperm.[6]

Very likely factors are involved in precipitation by charcoal which are not present when $(NH_4)_2SO_4$ and $BaCl_2$ are used. Very possibly the amboceptor is split by the charcoal; or, it may not be split until the acetone in the HCl reaches a certain concentration. In any case the cleavage of the molecule gives results identical with those gotten by Miss Woodward's methods.

C. REACTIONS TO HEAT

Lillie has shown that the agglutinating material is extremely resistant to heat. Exudate which has been boiled agglutinates spermatozoa perfectly well. It has, however, lost its capacity as a parthenogenetic agent (Woodward).

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[6] It is very important to guard against impurities in the charcoal. These after extraction with HCl give a voluminous precipitate with acetone.

On the one-body view we must reckon with the following possibilities: (1) a rupture of the molecule; (2) the destruction or alteration of the ovophile side-chain.

VI

Looked at conservatively, the methods of precipitation alone do not enable us to decide the one-body–two-body issue. The same thing may be said of the results of boiling. One conclusion, however, is certainly warranted: there is a constitutional weakness in the amboceptor so pronounced that this molecule breaks down with the greatest ease and, under very diverse conditions, always cleaves in a manner that separates the spermophile from the ovophile side-chain. Indeed one doubts whether the amboceptor can hold its ovophile side-chain after the agglutinating group has united with the receptors of the sperm. This, if true, would be awkward for the theory.

VII

D. FILTERABILITY

Lillie has shown that exudates which have passed through Berkefeld filters no longer agglutinate spermatozoa. The agglutinating material, in this case, can be recovered, as Miss Sampson found last summer, by washing the filter-cone in sea-water. In the original filtrate I was able to demonstrate lipolysin.

It is conceivable that the agglutinating material is not filterable because of "chemical adsorption." If this is true, then filtration becomes merely another method for the chemical decomposition of the amboceptor. Yet, we can account in this manner for only a portion of the agglutinin held back. It seems very unlikely that the fraction which can be recovered by merely washing the filter-cone, was held chemically bound. Moreover, on account of the metal band which holds the filter-cone in position, a remnant of the secretion invariably fails to pass through. This remnant has a higher agglutinating value than the original exudate. It seems safe to conclude that the agglutinating material is held back mechanically. If correct, these considerations based on filtration are conclusive, for we know of no cases in which a substance is chemically decomposed merely because the whole molecule is unable to get through the pores of a filter.

The results of filtration seem to me to necessitate the two-body view. None of the facts explicable by the amboceptor appear to become inexplicable when this body is analyzed into an agglutinin and a lipolysin. As for the difficulties of constant association, these are no greater in this case than the difficulties which arise because serum albumin and serum globulin always occur together in the blood.

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DESCRIPTION OF A PECULIAR YOLK MASS IN THE OVIDUCT OF A HEN

A DESCRIPTION of this specimen seems desirable for two chief reasons: First, because of its unique nature; second, because it supplies the data with which to answer the question whether reverse movement, possibly antiperistalsis, occurs in the formation of double eggs and similar anomalies.

The specimen was presented to the histological laboratory by Ashton Barbour, of Charlottesville, Va., six hours after it had been removed from an apparently normal year-old hen. He described it as having been taken from the ''egg-bag.'' When questioned, he was positive that he had noticed a number of developing eggs, ''little yellow balls,'' attached to the dorsal surface of the abdominal cavity. His anatomical observations stopped at this point.

The specimen was roughly egg-shaped, and of a yolk or yellowish-orange color. Between ends it measured 9½ cm. Its diameter at the point of greatest width (about one third the distance from the wider end) was 8 cm. When opened the mass was found to contain an egg of average size, with a shell of normal hardness and thickness. The egg was not exactly in the center, but was placed slightly to one side and towards the larger end, causing a variation in the thickness of the lateral walls of the enveloping mass (Fig. 1). At the thickest point the lateral wall was 2 cm. thick, at the thinnest point 1 cm. At the larger end the wall measured ¾ cm. in thickness, at the smaller end it measured 1½ cm. in thickness. The weight of the enveloping portion of this yolk mass, after the enclosed egg had been removed, was about 190 gms. The general ovoid shape of the mass was presumably determined by the enclosed egg.

The mass was made up of layers of yellow, yolk-like material